

# NOTES ON FEEDING BEHAVIOUR OF *VARANUS BENGALENSIS* (SAURIA: VARANIDAE)<sup>1</sup>

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(With seven text-figures)

The present study documents certain behavioural aspects of the feeding of *Varanus bengalensis*. Search patterns are emphasized, showing that this species exhibits both area- and object-concentrated foraging behaviour. Most successful area-concentrated foraging includes casting behaviour. The perceptual field is estimated, with mean reactive distance shown to be 1.3 m, and mean active pursuit distance 2.6 m. Flush-pursuit foraging behaviours are most common, with success ratios varying from 44 to 82 per cent, depending largely on prey type. Social facilitation is an important aspect of high predator densities, with piracy common, but with success dependent on size of the interacting individuals. The most common hunting modes are speculative, flushing, and open pursuit; stalking is rare.

## INTRODUCTION

A number of studies have demonstrated the importance of sensory modalities in predatory behaviour of reptiles (see Burghardt 1970, Herzog and Burghardt 1974, for pertinent reviews). Most students now realize that prey movement, colour, morphology, and predator experience are all relevant variables in prey selection (Ruggiero *et al.* 1979). However, few studies have analyzed the movements associated with predation by reptiles, as has been done with many species of fishes, birds, and mammals (see Curio 1976, for review). For the most part studies of reptile predation behaviour have been experimental and have focussed on aspects of chemoreception in prey capture (chiefly reviewed by Burghardt 1975, Burghardt and Pruitt 1975), focussing on the nature and role of innate chemical recognition of prey and the effects of experience.

Description of predation in reptiles are largely limited to isolated field reports and cursory observation (see Drummond 1979, for a notable exception), and almost all of them deal with snakes. Clearly, an understanding of the sensory and behavioural adaptations of predatory lizards demand more comprehensive and detailed descriptions than are presently available. The research reported here was an investigation of the ethology of the predation of the large varanid lizard *Varanus bengalensis* under captive conditions.

## MATERIALS AND METHODS

Twelve adult *Varanus bengalensis* were used as the basis of this study; two males and eight females (Av. total lengths during the study for males was 115 cm, for females 95 cm). All were long time captives, raised from hatchlings, thoroughly accustomed to conditions of captivity. All were kept in two greenhouses (156 m<sup>2</sup>) at the author's home in Gainesville, Florida. Each greenhouse contained five individuals (4 females, 1 male). While the females

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had been kept in specific greenhouses for several years, the males were often interchanged during spring to encourage reproductive behaviour, which was being studied at the same time (see Auffenberg 1981a, b). Each greenhouse was a seminatural situation, being provided with facilities for climbing, basking, and hiding. While most of the central floor area was clear, small rock and brush piles were located around the edges; a few plants and a log or two were near the center.

The data on which the study is based were gathered by videotape recording. One (sometimes two) video cameras (Panasonic WV-1300A) and time lapse recorders (NV-8030) taped the monitors' activity every day from 0800 to 1730 hrs for a period of three years. These tapes form the basis the present study as well as of the analyses already finished (Auffenberg, 1981a, b, on combat and courtship). As a result, aspects of the feeding behaviour of this species were recorded during a total of 250 feeding bouts. The completed tapes were scanned every evening by means of a fast playback feature and appropriate sections marked for later analysis.

On later review of pertinent tape sections, movements over the surface, as well as movements of parts of each monitor during food searches (head, tongue, front feet, etc.), could be traced off of the video screen (Panasonic TR-9001M) and direction, angles or rates of movement analyzed.

Four types of food were offered during the study — "carrion," turtle eggs, live white mice, and live frogs (*Rana utricularia*). The "carrion" was represented by pieces of dead laboratory rats; frozen and then cut into 16-20 pieces. Table 1 provides pertinent data on the physical characteristics of the prey.

Food was offered every two weeks during the warmer months, every four weeks in win-

ter. Carrion was usually randomly scattered about the greenhouse floors, turtle eggs randomly placed on the surface or buried with the top of shell 2 cm deep; live frogs and mice were thrown into the greenhouses in places where the monitors could not see them hit the surface. These methods of food presentation tended to generate strong, consistent search behaviours on the part of the resident monitors.

RESULTS

FOOD CONSUMPTION

*Satiation Level.*—Satiation level was determined on the basis of the monitors nudging the food with their snouts instead of eating it. For the adult males the mean total food weight at satiation level is 160.7 g ± 24.8 g; for females 99.8 g ± 15.7 g. These results are respectively 6.9 per cent of the mean body weight of the males (g) and 5.8 per cent of the mean body weight of the females (g). However, variability in total intake is great, being from 68.4 to 495.9 g for males (to 18.1% of total body weight). There is no correlation between amount eaten and food type.

*Handling Time.*—This period includes both manipulating the food (including killing it, if necessary) and swallowing. Both are clearly

TABLE 1

PHYSICAL CHARACTERISTICS OF THE PREY OFFERED TO *Varanus bengalensis*

Prey Type	n	X weight (gm) + PE	X silhouette size (cm <sup>2</sup> )
"carrion" (rat chunks)	38	17.1	10.5
turtle eggs	12	18.6	5.1
frogs	23	13.1	14.8
mice	27	26.7	16.2

positively related to food particle size. However, in the present study, the "carrion," live frogs, and live mice were all approximately the same size (Table 1).

Table 2 shows that mean handling time is least for "carrion," intermediate for live frogs, and very significantly more for live mice. On the basis of comparative review of the taped sequences, it is obvious that the increased handling time for live mice is largely due to the fact that frogs are often swallowed alive, with little or no attempt made to stun or kill

*tatus*, and *Anolis carolinensis*. All three species were eaten, though not commonly, for some individuals of particularly the last species remained in the greenhouses for several weeks and their remains were rare in the monitor droppings. Two successful attacks on *Anolis carolinensis* were observed; both after active pursuit on the ground. No attacks on *Eumeces* were witnessed, but their remains were sometimes found in monitor droppings.

*Leilopisma* were often taken, usually by a short pursuit and grab after having been flush-

TABLE 2  
HANDLING TIMES (SEC) OF VARIOUS FOOD TYPES

Food Type	n	O.R.	X	PE±	S.D.	t-test
"carrion"	129	0.6-20.4	3.7	1.8	5.0	not sig.
live frogs	112	0.9-14.4	5.2	0.9	1.1	highly sig. (df = 87,
live mice	88	6.9-28.8	16.3	3.1	2.4	t-test=3.17

them. On the other hand, live mice are quickly, but repeatedly dashed and/or scraped against the ground after being grasped. Unpublished data on feeding of adolescents of this monitor species (Ganci and Auffenberg MS) suggest that killing techniques are suited to prey size and the extent to which the prey can possibly injure the attacking individual.

*Other Foods.*--Several other prey taken, but not specifically offered as food, were noted and are worthy of mention. Ants were often eaten, but only a large species of carpenter ant (*Camponotus* sp.). These were obtained either when the monitors "rooted" through dry leaf litter with their snouts, or when the ants were moving in the open. In either case, these ants were usually picked up individually with the tongue, less often grasped by the jaws.

Three native lizards frequented the greenhouses: *Leilopisma laterale*, *Eumeces inexpectatus*, and *Anolis carolinensis*. All three species were eaten, though not commonly, for some individuals of particularly the last species remained in the greenhouses for several weeks and their remains were rare in the monitor droppings.

Two successful attacks on *Anolis carolinensis* were observed; both after active pursuit on the ground. No attacks on *Eumeces* were witnessed, but their remains were sometimes found in monitor droppings.

*Leilopisma* were often taken, usually by a short pursuit and grab after having been flushed from surface debris by the rooting monitors. Eggs of *Varanus bengalensis* were regularly eaten by the males (only), either when the eggs were strewn on the surface or placed in natural nests by the females. Young hatched naturally in the greenhouses were also sometimes eaten by adult males (only?). The largest *V. bengalensis* cannibalized was a female with a total length of 46 cm, by a male 121 cm total length.

Earthworms and beetle larvae were regularly eaten usually when digging next to rocks, logs, or in other damp places.

#### HUNTING MODES

Four major hunting modes were identified: random foraging, speculative foraging, stalking, and open pursuit. The first is discussed in detail below. Speculative foraging is not ran-

dom, but an area-concentrated search pattern (see below). It included *digging* in the soil or debris with the front feet, "*rooting*" through surface litter with the snout, and *flushing* by walking over or tonguing a small area. Speculative foraging in areas expected to produce prey was a common hunting mode. Most commonly it took the form of digging under and next to logs and rocks, or in the dampened soil under small leaks in the roof. Prey secured this way were earthworms and beetle larvae. For unexplained reasons, females dug more commonly than males (93.8% of 66 digging bouts were by the females). Even when a correction is made for the larger number of females, digging was largely a female activity (78.7% of all digging bouts). It may be related to nest selection, but there is no evidence for this.

Rooting was an activity equally practiced by both sexes. It consists of both lateral and anterior movements of the snout, moving the litter about in rather rapid, jerky movements. The behaviour may be related to the slit-like, posteriorly located nostrils in many *Varanus* species. Rooting results in the capture of earthworms, ants, lizards, and particularly beetle larvae. The latter is the predominant prey category of this lizard species in the wild (Auffenberg and Ipe 1983) and most are probably captured this way.

Flushing includes behavioural patterns in which a hidden prey is made to move. This was accomplished by scratching with one front foot, touching with the tongue, walking over the area quickly, and rarely during digging and rooting. It is a very effective hunting mode and may be speculative, or follow a pursuit sequence when the prey is momentarily lost to view. When the importance of flushing and distant visual recognition are compared in successful foraging bouts, only 35.0% of the total

successful captures of frogs and mice were accomplished by flushing the prey from a hiding place; 65.0% were visually spotted. For frogs, only 37.5% were flushed, 62.5% were caught after the frogs themselves moved. For live mice, the same ratio was 21.2% to 77.8%. Though the difference is significant at the 0.5% level, the reasons are not apparent.

Stalking of prey was very rare. When prey was seen, the attack was mounted from the detection distance, with no apparent attempt to shorten attack distance via a stealthy approach. Stalking by following a scent *trail*, particularly after flushing, probably occurs, though I found no evidence for it in this analysis.

Open pursuit was the most common hunting mode immediately preceding prey capture. Several important factors relating to open pursuit of both live frogs and mice were analyzed. These are: reactive distance and direction, chase distance, predation pursuit speed, prey speed (frogs and mice), and prey capture success ratio (Table 3). There are no significant differences in the successful pursuit of frogs compared to mice, or the mean visual reactive distance for each of these prey, or the mean chase distance for each prey species. However, prey escape speed is very different for the two prey species. The similarity of chase distances is due to the fact that the monitors grasp frogs anywhere on the body during their pursuit, but mice are almost always grasped on the side, resulting in the predator having to spend more time during the chase to get its head in an appropriate attack position. Frogs were attacked in mid-air during a jump, or immediately after stopping, when they frequently "froze." Freezing behaviour is clearly advantageous to frogs, for the attack success ratio on continuously moving frogs was 59%, while for those that freeze the ratio was 33%. Gregory (1979) considered immobility an im-

TABLE 3

FACTORS RELATED TO THE OPEN PURSUIT HUNTING MODE FOR LIVE FROGS AND MICE\*

Prey	X Visual Reactive Distance (m)	X Chase Distance (m)	Prey Speed m/sec		X Prey Diameter (mm)	Success (%)
			Normal	Escape		
Frogs	1.34±0.41	0.3±1.13	0.57	0.82	14	49
Mice		2.6±2.15	0.004	0.12		51

\* Prey density consistently 1/52 m<sup>2</sup>; frog n=112, mice n=88.

portant predator avoidance behaviour by *Rana aurora* and showed that distances to which potential predators can approach the frogs are positively correlated with predator size, while Heatwole (1968) proved that allowable predator approach distances are related to degree of cryptic coloration in anoline lizards. In this study, the majority of frogs remained completely immobile (81%) until actually touched by the snout or tongue of the *Varanus bengalensis*. The frogs flushed by *Varanus bengalensis* are chased again, apparently on the basis of visual, rather than olfactory recognition.

When caught, the frogs were usually scraped against the substrate a few times to move them into position for swallowing. Though no testable data are available, male *V. bengalensis* seem to have chased their prey at a higher rate of speed and appeared somewhat more motivated to capture them than females (see Auffenberg 1979, for other intersexual differences in the feeding of this species).

In contrast to frogs, more mice were captured when they froze (capture success for all moving mice 44%, for all frozen mice 82%), suggesting that scent probably plays a greater role in location of frozen mice than frozen frogs.

Mice were also grasped very specifically,

almost always on their side. They were then violently shaken, bitten repeatedly, and scraped and hit on the substrate. These observations were consistent with those of Loop (1974), who studied the attack and ingestion behaviours of *V. bengalensis* in considerable detail. Similar attack and ingestive behaviours depend on size of predatory snakes (Loop and Bailey 1972). Live mice often bit the predator on the side of the head, particularly on the area of the ascending maxillary process.

Mean reactive distances for mice in which the tongue was used to locate prey was 0.06 m ± 0.26 (n = 31). This distance is only slightly more than the length of the tongue itself and suggests that scent is important in locating prey only at close range. Gettkandt (1931), Kahmann (1932), Burghardt (1964, 1966), Herzog, and Burghardt (1974) all showed that prey movement was most important in eliciting attacks by snake predators and the same pattern seems operative in *Varanus bengalensis*. Figure 1 shows the average visual- and scent-reactive distances calculated in this species during the study. In addition, it illustrates the positions of prey resulting in pursuit. None of the pursued prey were located in the area included within 60 degrees on either side of the midline and behind the head. Thus the visual angle

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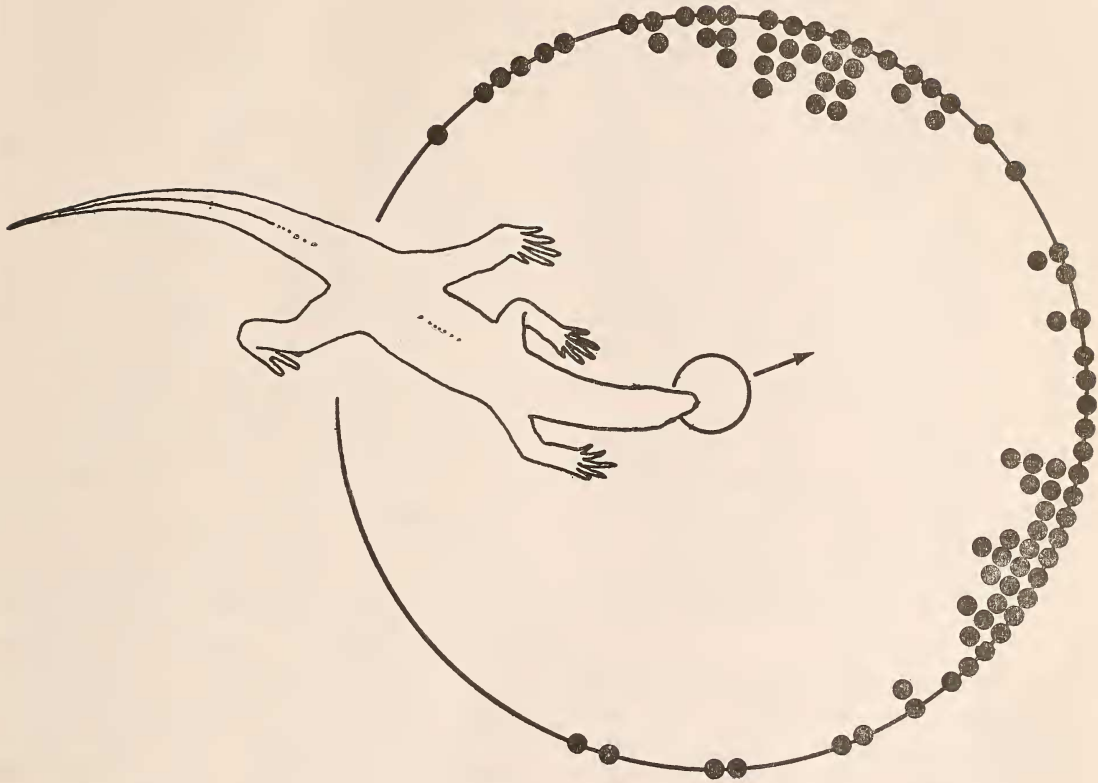


Fig. 1. Mean visual (outer circle) and scent (inner circle) reactance distances to prey in *Varanus bengalensis* ( $X = 1.34$  and  $0.12$  m respectively). The dots show the positions of those prey noticed and chased ( $n=88$ ) by the monitor in relation to the direction of travel (arrow).

important in foraging *V. bengalensis* is probably about  $240^\circ$ , or  $120^\circ$  on each side of the midline anterolaterally. The majority of reactances occurred with prey located within an arc of about  $90^\circ$  on each side, with most between about  $30^\circ$  and  $80^\circ$ .

SEARCH BEHAVIOUR AND FORAGING TACTICS

*Social Facilitation.*—The sight of one individual feeding often induced other nearby individuals to start feeding on their own, or in a common feeding area. The behaviour is well documented in various fish, bird, and mammal species (see Curio 1976, for review), but has

been only occasionally reported in reptiles (Greenberg 1977 Auffenberg 1981c). In monitor lizards it is common in particularly those species feeding in aggregations at large carrion, such as *Varanus komodoensis* (Auffenberg 1981c). In the *Varanus bengalensis* used in this study social facilitation often took the form of piracy, a form of which has previously been studied in birds (Hatch 1970).

Piracy among *Varanus bengalensis* normally occurred when one individual had prey in its mouth. Analyses of piracy observed in this study ( $n=45$ ) show that, in general, it was an

unsuccessful tactic (success percentage 26.7). However, success level was largely determined by the sizes of the interacting individuals. Thus piracy acts against smaller individuals by larger ones was frequently successful (62.5% of all such interactions). However, most piracy attempts were conducted by smaller ( $n=33$ ) than by larger individuals ( $n=12$ ), though usually unsuccessful ( $n=33$ , 84.8% failures), regardless of the victim's size; and even less successful when the victims were larger than the pirates ( $n=23$ , 87.0%). Attempted piracy among more or less equal-sized individuals was usually unsuccessful ( $n=14$ , 28.6%).

Food particle size was also clearly important, for when the food particle diameter was larger than 14 mm and length greater than 50 mm, pirating attempts were more successful ( $n=13$ , 81.0%) than when food particles were smaller ( $n=20$ , 19.0%) and handling time was short.

Piracy attempts were not particularly rewarding when food was plentiful, for other individuals were often drawn to the area of piracy attempt, and these individuals may feed on

the surplus food, while the potential (usually unsuccessful) pirate is chasing another. Piracy attempts were also characterized by a chase and/or grab at the mouth—sometimes even when the other mouth had nothing in it. It was also more common by certain individuals than by others of equal size.

*Search Movements.* — Locomotion during which there is no search for food was noticeably different than that while looking for food. The primary differences during food search were (1) more rapid and regular tongue flicking, and (2) greater lateral head and body movements. Nonforaging locomotion was usually practiced when individuals moved between the retreat and basking sites. These trackways were usually direct, with few and generally small deviations; mean forward speed was 9.0 cm/sec. On the other hand, trackways made by foraging individuals were less direct, often convoluted, circular or sinuous (Fig. 3). Mean forward speed was the same (8.1 cm/sec). The head is rhythmically swung from one side to the other (=scanning), with tongue-flicking usually occurring at the end of each lateral

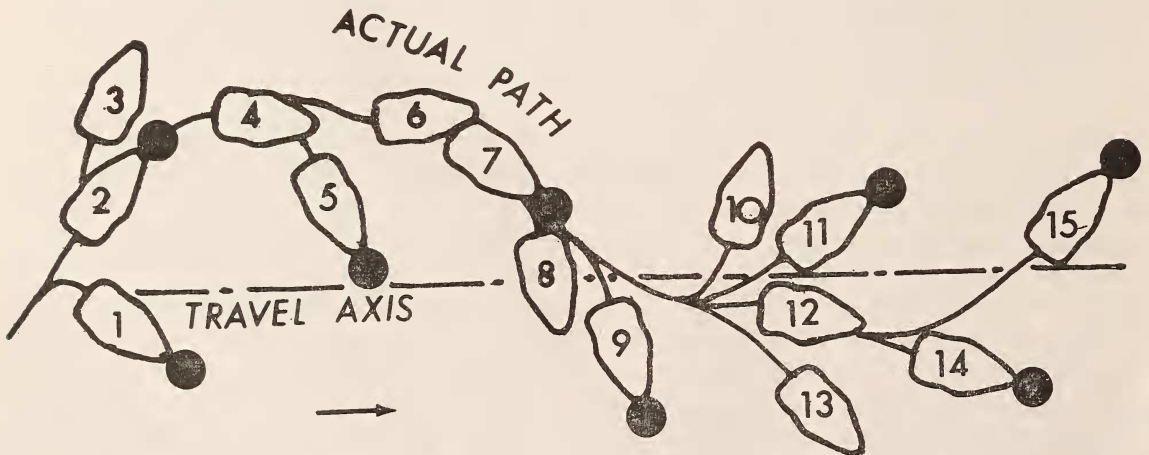


Fig. 2. Typical scanning movements during foraging. Numbered heads show positions at one-second intervals; dots show points at which tongues have been flicked; travel axis and actual path both indicated.

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swing (Fig. 2). A special form of scanning in small areas is called casting (see Curio 1976, for discussion of its use in invertebrates). In casting the forward movement is stopped

entirely (or nearly so), with exaggerated lateral head sweeps and (in varanids) with more tongue flicks (Table 4). Tongue flicks in non-foraging movements usually occur at the

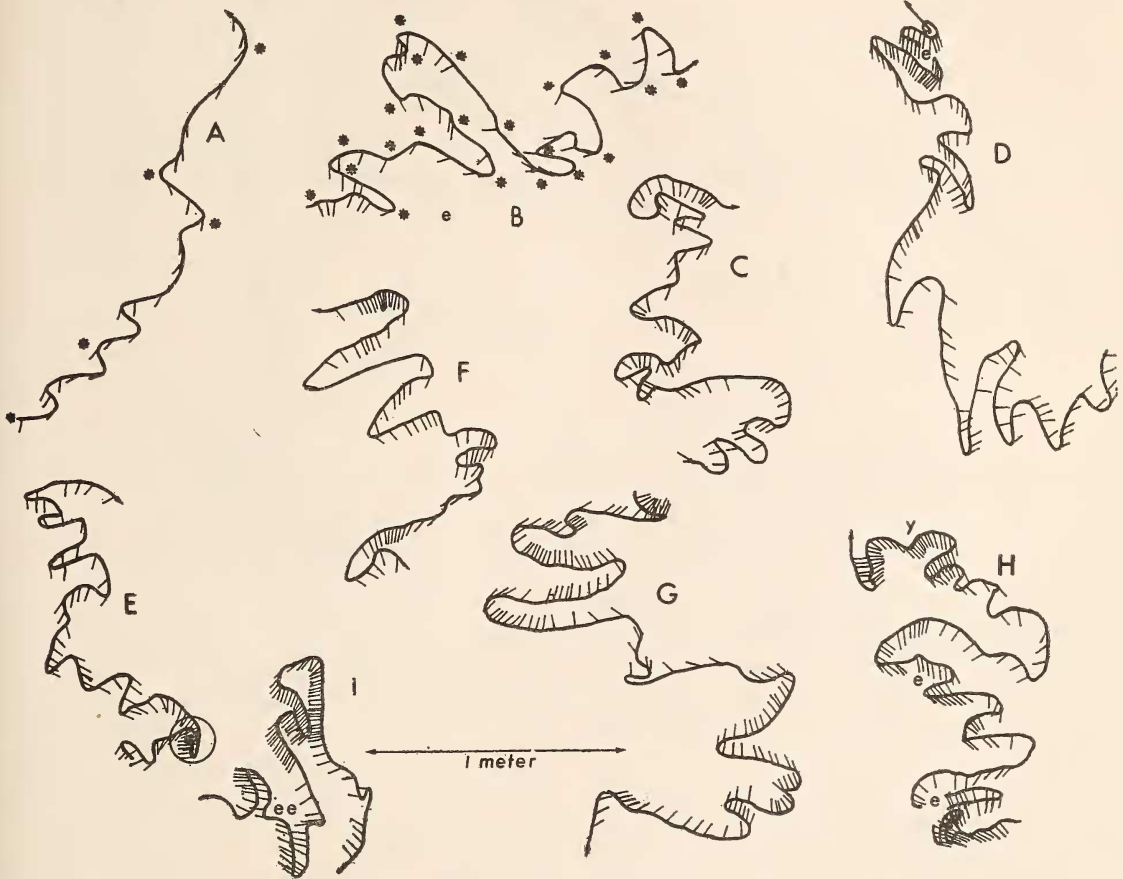


Fig. 3. Typical locomotor patterns. Scale indicated. Head positions shown as short lines, with continuous line tracing movement of snout tip; arrow showing direction of body movement. Dots indicate tongue flick locations; X shows food locations (see text). A, non-foraging pattern, without scanning; B, foraging pattern with typical increasing tonguing during wide lateral scanning movements, e, to right being position of buried turtle egg (not found), non-area-concentrated pattern; C, same, but foraging more intense as seen in slower movements and rate of forward progression; D, same, but with more intensive, slower search near buried turtle egg (e, located and eaten); E, same, near wet spot on greenhouse floor (circle); F, alternating low and high intensity area-concentration pattern; G, same, more intense with slower greater lateral movement; H, pattern in which two buried turtle eggs (e) are found and eaten, and place where egg found by same individual the day before (y); (I) pattern preceding and following successful location of two pieces of meat (ee).





Fig. 4. Components comprising the maximum food search path of *Varanus bengalensis*: NB = maximum lateral undulations of neck and body (c. 7 cm on either side of travel axis), H = lateral movements of head, c. 5 cm, T = lateral movements of head, c. 5 cm. Total width of scent discrimination path about 34 cm.

greatest extent of the head swings (sometimes during the mid-swing distance) (Fig. 3A). During foraging the tongue flicks occur more rapidly (Table 4), usually at several places between the greatest lateral movements of the head (Fig. 3B).

The lateral head scanning movements are functionally increased by the tongue length, for it is usually completely extended with each flick (max. distance about 5 cm in adults). In addition, the amplitude of the lateral movement of the body is 5-10 cm (Av. = 7.3); the "wave length" of the lateral head swings is one per 10-80.3 cm, depending largely on lizard length (Av. = 63.2 cm). Figure 4 illustrates the extent of the major movements contributing to the total width of the search path in *Varanus bengalensis* adults. The mean head movement per second in casting is about 40% slower than that when scanning, and 69%

TABLE 4

COMPARISON OF MOVEMENT PATTERNS DURING THE SEARCH FOR FOOD AND OTHERWISE

	Nonforaging (n=31)	Foraging (n=28)	
		Scanning (n=12)	Casting (n=16)
X Forward Speed (cm/sec)	9.0	8.1	0.2
X Lateral Head Sweep (total side-side) (in cm)	8.0	10.2	25.6
Distance of Head Movement/sec (in cm)	1.1	0.6	0.3
X No. Tongue Flick/sec	7.2	3.8	2.3

slower than when not foraging (Table 4). Thus both head movement and forward progression is slowed down as foraging intensity is in-

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creased, and tonguing becomes more rapid. Casting movements are slower and with a greater lateral component than other patterns (Table 4).

*Area-concentrated Search Patterns.*—*Varanus bengalensis* shows typical area-concentrated search behaviour, especially in reference to casting search patterns. Area-concentrated patterns using casting techniques typically alternate with scanning patterns during the search

for food. Figure 3 provides typical examples (Fig. 3D-I). A comparison of the non area-concentrated search pattern of Figure 3B, with area-concentrated types seen in parts of particularly patterns D through I clearly shows the slower movements and more complete investigation of the surface in the area-concentrated types. The scent of buried turtle eggs leads to area-concentration by casting, each at places where a buried egg was found the day before

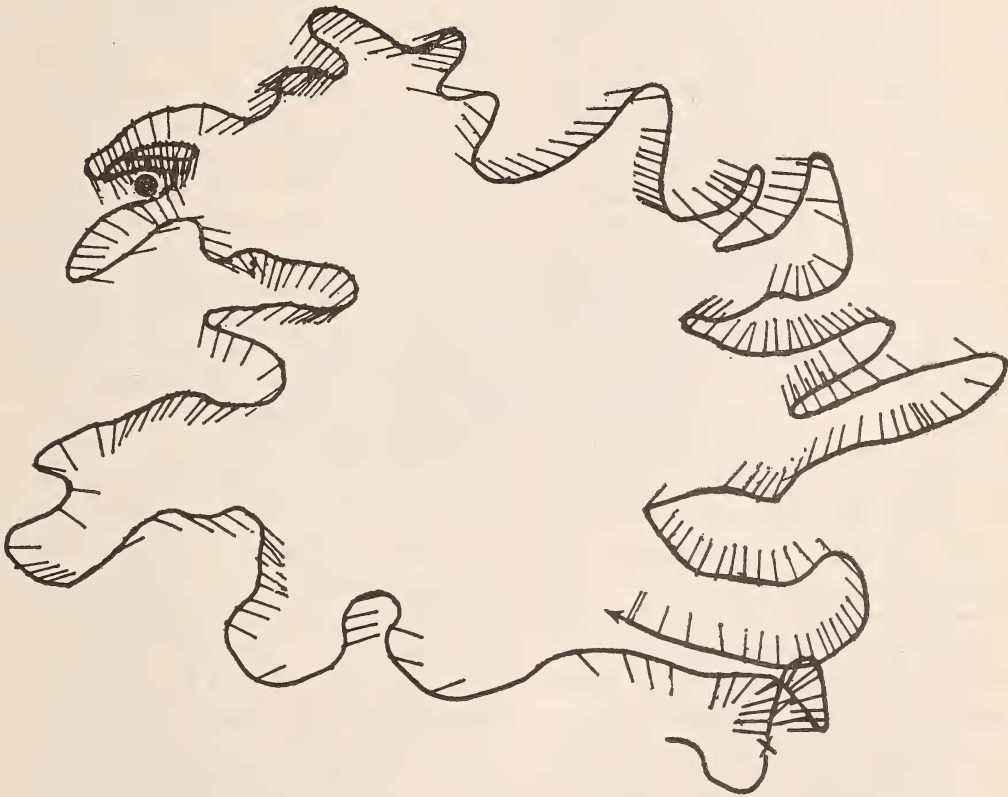


Fig. 5. Example of an extensive area-concentrated search brought in an area (dot) where a live mouse had been captured 24 hours previously, then returning by way of a rather circular path to the spot (X) where another live mouse had been captured at the beginning of the sequence shown. Maximum diameter of search path shown 2.1 m, total elapsed time 321 sec.

(Fig. 3H). Such area-concentrated searching as evidenced by casting clearly begins some distance (10-80 cm) before the food site (distance undoubtedly related to olfacient strength). Note that in Figure 3B a foraging monitor failed to find and eat a buried turtle egg at E, though it came within 30 cm of the location on two scanning sweeps; the travel rate and direction, as well as the tonguing frequency, all suggest it did not detect the food.

Figure 5 also shows another feature of the area-concentrated foraging pattern—that the successful location of food is not only preceded by, but also usually succeeded by casting. Direction changes after food discovery are not significantly different than changes before food detection, unlike the hunting behaviour reported in some birds (Smith and Dawkins 1971). However, the arc produced in casting has a mean radius of 1.2 m before discovery, a radius of 0.7 m after discovery, with a proportionately smaller variance. Scanning movements are greater near a scent focal point (X scanning width 28 cm) than they are when the monitor is far from the focal scent area (X = 15 cm).

Intense area-concentrated search patterns occur when adult males respond to crossing the track of a female. The major difference in this pattern and that of a generalized, non-concentrated pattern, such as Figure 3B, is the former's more convoluted path and the alternation between more rapid and less rapid head movements as the pattern shifts from high to low intensity area-concentrated search patterns.

Figure 5 shows the resulting area-concentrated search pattern when food is repeatedly located in fairly small area. Even without repeated food discovery in one area, there is a tendency for *Varanus bengalensis* to spend more time in places where it found food earlier the same day, or even on previous days. As an

example, in a sample of nine food search bouts randomly selected from the tape (total 6 hrs, or 21,776 sec, Av. bout length 40.3 min., or 2419 sec), individuals spent an average of 31.6% of the total search time at places where they had found food earlier in the same bout. This entire time was spent casting over the discovery area, with frequent tonguing of the soil and leaf litter (5.4% of the time was spent at food sites during earlier bouts; 3.3% of the time was devoted to activities unrelated to food discovery; 59.7% of the time was spent in areas where no food had previously been found). Statistics important in analyses of the situation are: each greenhouse floor has an area of 7 m x 7 m (49 m<sup>2</sup>), marked in square metre squares, in which food was offered and behaviours of the monitors taped. Nine feeding bouts were photographed, providing a maximum possible surface for movement of 441 m<sup>2</sup>. But of these only 181 m<sup>2</sup> were visited (41.0% of total), probably due to the fact that carrion food particles were located on only 30 squares (6.8% of total area available). The difference between the visitation of 181 and 30 (difference = 151 squares) is due to both random food search and movement from one food source to another. The 30 squares provided with food at one time or another were visited 105 times, including 75 revisited a second (or more) time, and only 8 never revisited again. Of the squares traversed (310) that never had only food (280), 82 were revisited a second (or more) time, and 77 were never revisited after the final crossing. This more or less equal distribution regarding non-food square transverses suggests these movements are random. However, the high order of revisits to squares in which food was found earlier (that same bout, or a subsequent one) suggests a very significant non-random site-specific pattern related to

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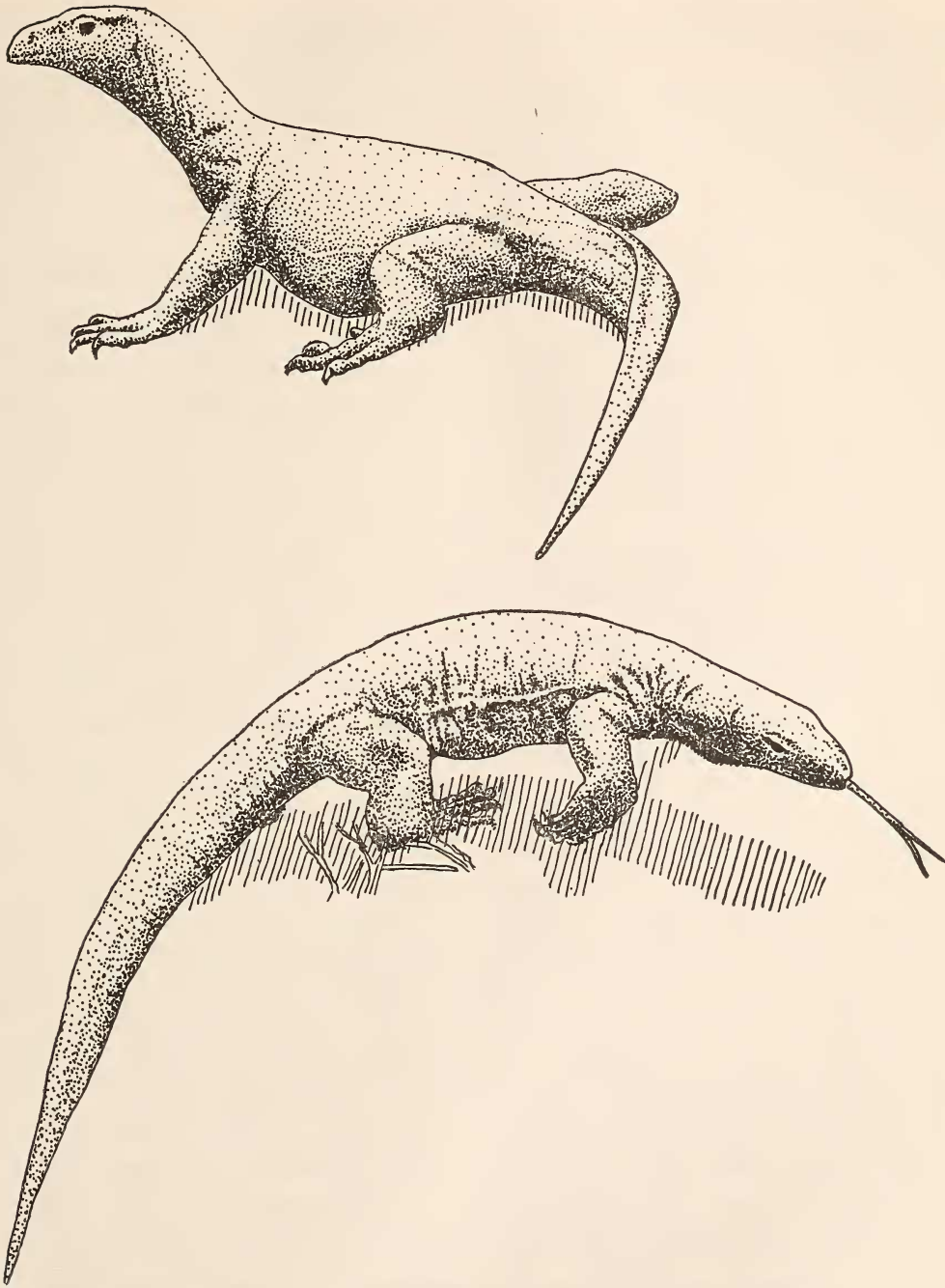


Fig. 6. *Varanus bengalensis*; above, attentive posture when engaged in an object-concentrated (entirely? visual) search for jumping frogs; below, normal body position during an area-concentration (largely olfactory) search for buried turtle eggs.

previous successful food location ( $X^2$  34.46,  $df = 1$ ,  $P = 0.001$ ).

*Object-concentrated Search Patterns*—In many circumstances it is difficult to distinguish between area- and object-concentrated search patterns, especially when the search for food is obviously largely scent-dominated. One example is when the intensive search for an object (female, buried turtle eggs, etc.) takes place in a small area. Digging next to and under logs and rooting in leaf debris for insect prey are other examples. However, in other circumstances concentration on a particular object is clearly divorced from concentration on a place. This perhaps is best illustrated in the quite different search for larger active prey, such as living frogs and mice.

During the search for moving prey the tongue is rarely used. The head is held high, though parallel to the ground (Fig. 6). The entire demeanour appears tense and alert, with the head often turned quickly from side to side. Likely movements within several metres lead to a rapid dash in that direction, and the prey is often chased for some distance. Loss of visual contact through freezing or hiding behaviour of the prey usually leads to intense area-concentration behaviour with tonguing and rooting of the surface litter in a small area until the prey is flushed or found. Neither time budget nor space utilization analyses during object-concentrated searches show any significant positive relationship with previous successful capture sites—at least within the confines of the greenhouses used in this study. However, field investigations would undoubtedly show that object-concentrated hunting modes lead to selection of specific habitat types and probably at specific times of the day, as they do in *Varanus komodoensis* (Auffenberg 1978, 1981c). Though no comparable studies have been conducted on reptiles, research on other verte-

brates (i.e., birds and mammals) has shown that specific hunting behaviours are affected as a consequence of remarkable few experiences by the predator (Croese 1970, Randall 1970).

#### DISCUSSION

One of the results of this study is that the satiation level has been shown to be much higher for adult males than for adult females, agreeing with earlier data that during adolescent growth the males of this species tend to consume more food than females of the same age class (Auffenberg 1979). This suggests that males may process food faster than females and thus help to explain why males tend to bask longer than females (Auffenberg 1979). The fact that male *V. bengalensis* eat more food per unit time than females suggests that males are exposed to higher predation levels by larger carnivores, and thus the faster growth of males probably results in a differential mortality in the sexes. This should be checked by appropriately designed data obtained from field studies.

Handling time is significantly lower for carrion type food than live prey; particularly those prey species, such as mice, that are capable of injuring the predator. These and other data clearly show that attack techniques are suited to prey type, as has been shown to be the case in the Komodo monitor (Auffenberg 1981c). Unpublished data on captive adolescent *V. bengalensis* suggest that these techniques are developed quickly and very early, requiring a remarkably short time for development (Ganci and Auffenberg, MS).

Foraging behaviour of this species includes a great amount of rooting in the surface litter. The way in which this is done plus the similar behaviour of other slit-nostriled varanids (*Varanus rudicollis*, *V. grayi*, *V. dumerilii*)

and apparent absence of such behaviour in the round-nostriled forms with which I am familiar (*Varanus komodoensis*, *V. varius*, *V. salvator*; all in author's field notes) suggests there is an important functional relationship requiring additional confirmation.

The ambush tactic is apparently not used by *Varanus bengalensis* of any size to obtain prey. However, in *V. komodoensis*, the adults regularly practice this technique, while the young or even half-grown individuals do not (Auffenberg 1981c). I conclude that ambush hunting is a behavioural pattern only regularly practiced by very large monitors hunting proportionately large prey. It may, in fact, be restricted to only adult *V. komodoensis* as a regular hunting tactic among at least varanids.

On the other hand, open pursuit of prey much smaller than their own mass is a common behavioural mode in *Varanus bengalensis*, as it seems to be in most (all?) other monitor species, including all sizes of *V. komodoensis*. Open pursuit often follows a deliberate object-oriented search pattern—frequently initiated by visual prey recognition from a distance. Similar hunting modes have been reported for varanids in the field (Auffenberg 1981c), and we must conclude it is one of the most important techniques for food procurement by at least the more active species of the family (there is no evidence that it occurs in *Varanus grayi*, as an example, author's field notes).

Area-concentrated search patterns are also important, particularly for small, inactive live prey (beetle grubs, etc.) and carrion. In this mode, scent apparently plays a major role in food location. It may be accompanied by rooting, digging, scratching, and similar surface disturbance techniques designed to flush or disclose the prey. Tonguing is frequent and casting behaviours are characteristic during high intensity search for particularly carrion.

The ability of varanids to locate carrion from great distances (*c* 10 km) has been reported in *Varanus komodoensis* (Auffenberg 1981c) and from lesser distances in *Varanus salvator* (Auffenberg 1980). Though *V. bengalensis* apparently feeds on less carrion in the wild than do these two species (Auffenberg, in press), scent-oriented, area-concentrated patterns are utilized in its location. Furthermore, the present study makes it clear that individuals frequently return to area in which they have found food previously. The same pattern has been demonstrated for *Varanus komodoensis* in respect to ambush locations for large prey (Auffenberg 1978, 1981c). Long-lived lizards, such as *V. bengalensis*, would clearly profit from long-term area-concentrated search patterns, for longevity provides the accumulation of experience necessary to concentrate their feeding forays in those areas where prey are either actually more abundant, or attack is facilitated by peculiarities of prey behaviour or local topography. This is clearly demonstrated in the behavioural relationship of adult *V. komodoensis* and the deer and pigs on which they regularly feed (Auffenberg 1978, 1981). In *V. komodoensis* species ambushes are usually performed in areas of high prey concentrations, even when such concentrations occur only during short parts of the day. On the other hand, there is some evidence that younger Komodo monitors are not as area-oriented as are the adults, and this seems to be the case in *V. bengalensis* as well, though proof is lacking. If true, then it suggests that area-concentration and, particularly, one prey-one place associations take a long time to develop. However, the tendency to return to successful hunting sites is clear, even if the successful encounter was several weeks previous. In the Komodo monitor there is evidence that the location of such successes may be remembered for at least

several months. It is even possible that many of the ambush sites visited over several days foraging may represent a series of previously successful prey encounter sites and that the consistency of the foraging foray movements may be based on such earlier successes. This study has shown that in *Varanus bengalensis* about one-third of the time spent in a foraging bout is spent at previous successful food encounter sites.

It has been shown above that the perceptual field of *Varanus bengalensis* is greatly widened by the rhythmic lateral bending of the head and body. But the actual field recognized is probably similar to that demonstrated for herring larvae (Rosenthal and Hempel 1970), being in the form of an undulating tube (Fig. 7). Curio (1976) has suggested that similar lateral movements in fishes tend to increase the mean diameter of the predator, thus increasing

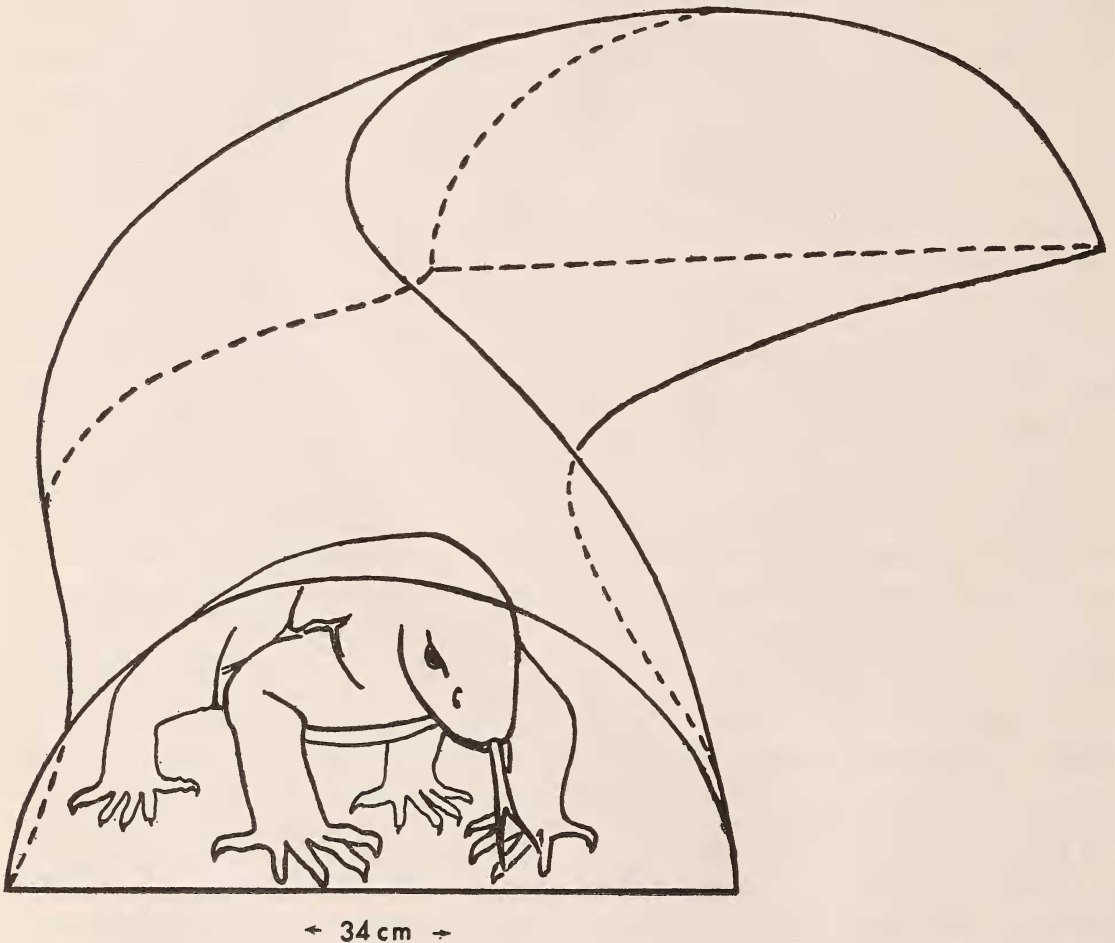


Fig. 7. Diagrammatic representation of presumed undulating perceptual tunnel about 34 cm wide in adult *Varanus bengalensis* (adapted from illustrative concept of Rosenthal and Dawkins, 1970).

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their discrimination efficiency. This is clearly the case in *Varanus bengalensis*.

While the present study has helped elucidate certain factors regarding the behaviour of foraging monitors in the field, many important questions remain. Most of these can be answered only after more thorough study in both the field and laboratory. To date most studies of the ethology of predation have used insects, birds, fishes, and mammals as subject groups. Little work has been done in this field with

reptiles. Yet, there is much about reptile behaviour suggesting that the patterns in this group are not the same as have been demonstrated previously (see Curio 1976). Hopefully this report will stimulate others to further investigate the feeding strategies of particularly the snakes, in which notoriously little has been reported, but for which much good work could easily be done in the laboratory in view of their general adaptability to captive situations.

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